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SLOW AND RAPID GROWTH¹

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The growth rate of plants and of plant organs resembles the rate of a monomolecular chemical reaction (Reed, 1920 *a*). Having obtained a mathematical expression of the growth rate, it should be possible to analyze the process into some of its main components. It has been found that the growth rate of certain organisms may be expressed by the differential equation

$$\frac{dx}{dt} = k(a - x),$$

where x represents the size of the organism at time t , a represents the final size attained, and k is a constant of the reaction. The rate at any given time is, therefore, proportional to the amount of growth yet to be made. It is accordingly rapid at the outset and becomes slower as the end of the growth period is reached.

The integral form of this equation is

$$x = a(1 - e^{-kt}),$$

from which the size of the organism at any time may be calculated. If the above assumption is correct, the calculated value of x should not be widely divergent from the observed value for the same time. As a matter of fact, the two values have been found to agree very well. It seems profitable to extend this method of inquiry into different phases of the problem of growth, in the attempt to gain further information on the dynamics of growth.

Measurements of a selected number of shoots on young apricot trees were made throughout the growing season. The mean length of the shoots at each interval of measurement was taken as the observed length at that particular time.

The shoots were of two sorts, and measurements were separately made upon each. The first were on trees which received no pruning; the second were on trees which received, annually, a severe pruning, with the result that the new shoots grew very much more rapidly than those on the unpruned trees. Both classes of trees are in adjoining rows in the orchard and receive the same cultural treatments with the exception of pruning.

At the outset, 50 shoots were selected for each class, but the number was reduced by various accidents during the summer, with the result

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that there were 33 shoots in the unpruned class and 28 in the pruned class. In either case the number of variants is large enough to give a satisfactory mean.

TABLE I. *Mean Length of New Shoots on Pruned and Unpruned Apricot Trees During one Season*

<i>t</i>	On Unpruned Trees		On Pruned Trees	
	<i>x</i> (Observed)	<i>x</i> (Calculated)	<i>x</i> (Observed)	<i>x</i> (Calculated)
weeks	cm.	cm.	cm.	cm.
1	9	10	13	23
2	17	20	37	43
3	25	28	60	61
4	29	36	73	78
5	34	42	88	92
6	42	48	102	105
7	50	54	113	117
8	57	59	121	128
9	63	63	132	137
10	68	67	142	145
11	71	70	148	153
12	77	73	156	160
13	79	76	163	166
14	82	79	174	171
15	83	81	177	176
16	84	83	182	181
17	85	85	186	184
18	86	86	190	188
19	87	88	194	191
20	88	89	197	194
21	89	90	200	196
22	90	91	203	199
24				
25	94	94	208	204
26				
27			210	207

Table I contains the observed lengths of the two classes of shoots on the successive weeks of measurement. The mean final length of shoots on the unpruned trees was 94 cm., and that of shoots on the heavily pruned trees was 210 cm. We may let 100 represent the limiting value of x_1 and 218 that of x_2 . By a series of approximations the equation

$$x_1 = 100(1 - e^{-.11 t})$$

was found to be satisfactory for the values of the shoots on the unpruned trees, and

$$x_2 = 218(1 - e^{-.11 t})$$

for the shoots on the pruned trees. A graphic comparison of these values is given in figure 1.

It will be seen that the only difference between the two integral equations is in the value of the constant a . The value of k , the constant of the reaction, is the same in both cases. The values of x calculated from these

equations (table 1) are seen to be very close to the observed values with few exceptions; the values, therefore, may be assumed to be approximately correct.

A series of values more nearly corresponding to the observed lengths may be obtained by the means employed in another study (Reed, 1920 *b*) of this kind, but the simpler equation gives satisfactorily close values and its use will contribute to clarity of discussion.

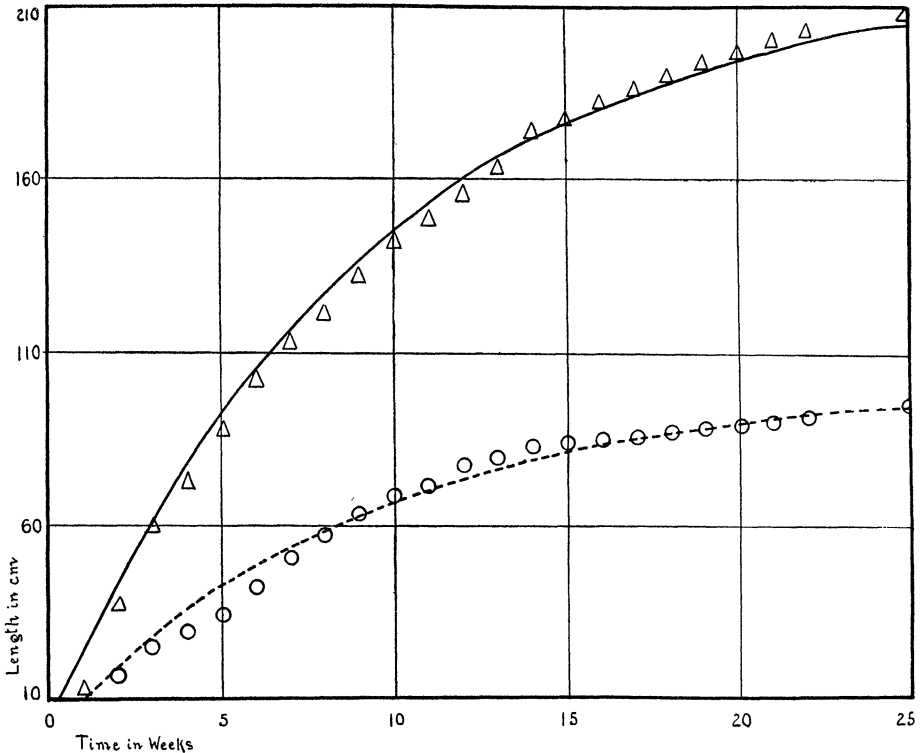


FIG. 1. Curves showing mean length of apricot shoots during one season.

△ △ △, Observed lengths of shoots on pruned trees.

—, Length of shoots calculated from $x_2 = 218(1 - e^{-.11t})$.

○ ○ ○, Observed lengths of shoots on unpruned trees.

- - - -, Length of shoots calculated from $x_1 = 100(1 - e^{-.11t})$.

The differential equation, $dx/dt = k(a - x)$, represents rate of growth, *i.e.*, amount of elongation in unit time. If we get the weekly increments in length, we shall have the observed increments in unit time expressed as a rate per week, and can compare them with values calculated from the above differential equation. Since there are inevitable fluctuations in the actual growth rate, it will be better to use "adjusted" values, *S*, of the observed increments. This is a *slope* method of determining the observed values of

dx/dt and has been applied to statistical problems by McEwen and Michael (1919). Its usefulness depends upon the fact that the slope of the chord of a simple curve is approximately equal to that of the tangent at the point midway between the extremities of the chord. The values of S are obtained from $\frac{1}{2}$ (observed length at time $t + 1$ - observed length at time $t - 1$), which represents the average rate between time $t + \frac{1}{2}$ and time $t - \frac{1}{2}$. Figure 2 shows the values so obtained compared with the calculated rate. They show that the rate is at a maximum at the inception of the growth period and follows the course of a curve decreasing exponentially to the end of the period.

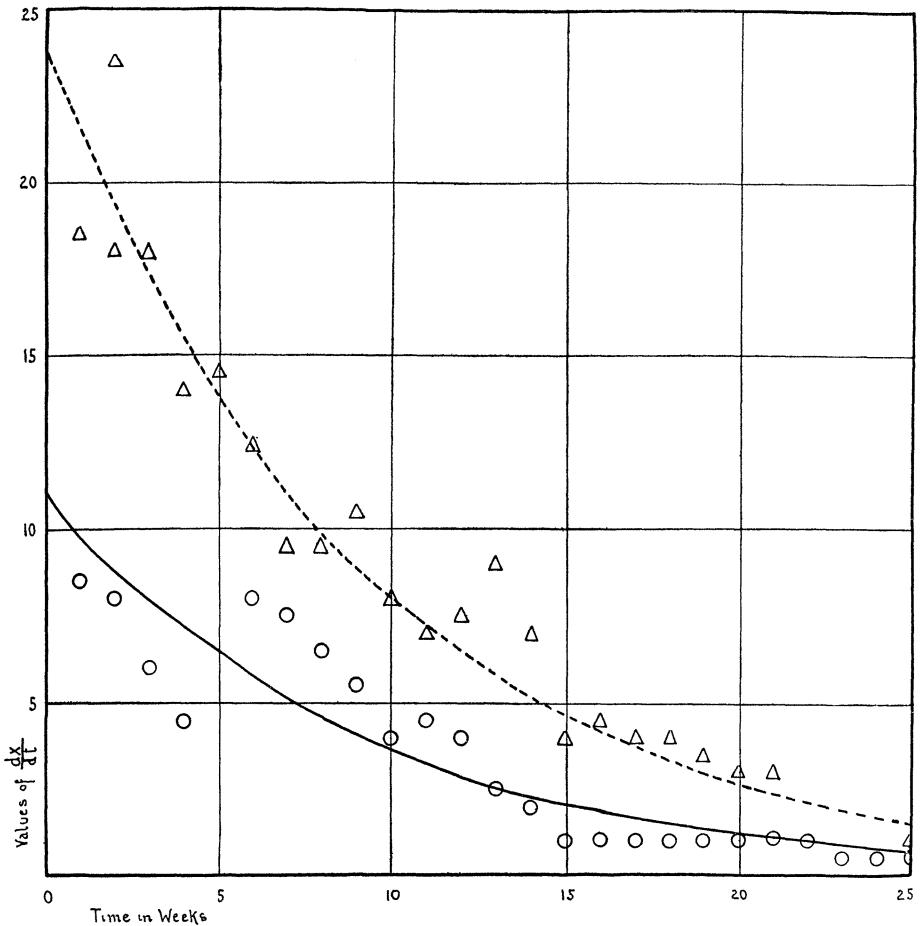


FIG. 2. Curves expressing rate of growth of apricot shoots.

$\Delta \Delta \Delta$, Observed growth increments (S) of shoots on pruned trees.

-----, Values of $dx/dt = .11(218 - x_2)$.

$\circ \circ \circ \circ$, Observed growth increments (S) of shoots on unpruned trees.

————, Values of $dx/dt = .11(100 - x_1)$.

From these results, it is plain that the quantitative difference between the two classes of shoots existed from the very outset, and that the greater total growth of shoots on the pruned trees was due to their faster growth in the early part of the period. This conclusion accords with the results of Pearl and Surface (1915), who showed that the superior plants in a population are, as a rule, superior from the seedling stage, and that the inferior members of the population are likewise inferior from the beginning.

This raises an important physiological question, *viz.*, How did the pruning of one lot affect the growth process in such a way that they made so much more rapid growth as soon as activity began in the spring? In other words, what happened to cause one lot to grow three times as fast as the other in the second week?

Referring to the differential equation expressing the rate, it will be seen that the rate in unit time is equal to the product of two quantities. The first quantity is k , the constant of the reaction, and the other is $(a - x)$, the difference between a constant and the length of the shoots at time t . The rate of growth of the two classes of shoots differs, then, only by the value of the second factor, *i.e.*, $(a - x)$. From the data, it seems probable that k , the constant of the reaction, is determined by the genetic constitution of the tree. It is well known that its value is determined from

$$k = \frac{1}{t} \log \frac{a}{a - x}.$$

The quantity $a - x$ is, therefore, the one whose value was altered. Now, from the integral equation

$$x = a(1 - e^{-kt})$$

it is easy to see that

$$a - x = ae^{-kt},$$

which means that the values of $a - x$ are equal to the product of a by an exponential function of the time. Since in both the unpruned and the pruned trees the value of e^{-kt} was the same, it is, therefore, plain that the value of $a - x$ is dependent upon the value of a . While the value of a must be, in a measure, determined by hereditary factors, it seems also subject to the influence of outer environmental factors such as those here operative.

In short, the rate of growth of the shoot appears to depend upon its final length. Whatever, therefore, contributes to the production of the ultimate length of the shoot influences the rate of growth from the beginning of the season.

The close correspondence between the growth of the shoots and the equations above stated is evidence that their growth is some sort of a catalytic process. According to this view, the organism is the end-product of a process in which a catalyst acts upon a substrate.

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